

Gonatus ursabrunae and *Gonatus oregonensis*, Two New Species of Squids from the Northeastern Pacific Ocean (Cephalopoda: Oegopsida: Gonatidae)

by

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Abstract. Two new species of gonatid squids are described from the northeastern Pacific. *Gonatus ursabrunae* spec. nov. is distinguished by the presence of greatly enlarged suckers in two locations: in the lateral rows of the middle portions of arms I-III, and in the proximal portion of the dactylus. This species has been taken off Oregon and west to the central Aleutian Islands. *Gonatus oregonensis* spec. nov. is characterized primarily by the number of club suckers, greater than in any other *Gonatus* (*s.s.*) species. This species has been taken only off Oregon. The status of systematics in the family is discussed and the species compared. Based on existing collections, up to three additional species of Gonatidae may remain undescribed in the North Pacific, and one in the Antarctic. *Gonatus phoebetriae* Imber, 1978, is shown to be a *nomen dubium*.

INTRODUCTION

THE FAMILY Gonatidae is of major importance to the ecology of the Subarctic Pacific; species of this group dominate the pelagic cephalopod fauna in this area (JEFFERTS, 1983; KUBODERA & JEFFERTS, 1984), and are important in the diets of seabirds, fishes, and marine mammals (LEBRASSEUR, 1966; SANGER & BAIRD, 1977; FISCUS, 1982). Greater knowledge of the taxonomy of gonatids is vital to an understanding of broader ecologic questions in the Subarctic Pacific.

Three genera are currently recognized in the family: *Gonatopsis* Sasaki, 1920, *Berryteuthis* Naef, 1921, and *Gonatus* Gray, 1849. *Gonatopsis* is distinguished by the loss of tentacles in the adults. The following species are recognized: *Gonatopsis octopedatus* Sasaki, 1920, *G. borealis* Sasaki, 1923, *G. makko* Okutani & Nemoto, 1964, *G. japonicus* Okiyama, 1969, and *G. okutanii* Nesis, 1972. Another form of *Gonatopsis*, type A of KUBODERA (1978) has been described, but not named. *Berryteuthis* is characterized by the absence of club hooks, a septemdentate radula, and a carpal-locking zone that extends up onto the manus and dactylus as a "fixing apparatus" (BERRY, 1913). Two species are presently recognized: *Berryteuthis magister* (Berry, 1913) and *B. anonychus* (Pearcy & Voss, 1963).

The taxonomy of *Gonatus* has recently been in a state

of flux. The genus is characterized by a quinquedentate radula and a carpal-locking zone consisting of alternating ridges with large suckers medially and grooves with fleshy knobs medially. Prior to 1972 only two species were recognized: *G. fabricii* (Lichtenstein, 1818) and *G. antarcticus* Lönnberg, 1898. *Gonatus berryi* Naef, 1923, had been forgotten until YOUNG (1972) revived usage of the name and redescribed the species. *Gonatus kamtschatica* Middendorff, 1849, was originally inadequately described on the basis of a specimen no longer extant, and has been declared a *nomen dubium* (KUBODERA & OKUTANI, 1981a). Since 1972 seven new species have been described: *G. onyx* Young, 1972, *G. pyros* Young, 1972, *G. californiensis* Young, 1972, *G. tinro* Nesis, 1972, *G. madokai* Kubodera & Okutani, 1977, *G. middendorffi* Kubodera & Okutani, 1981a, and *G. steenstrupi* Kristensen, 1981. Two others have been described, but not named: *Gonatus* type C of KUBODERA, 1978 (synonym, *Gonatus* type A of KUBODERA & OKUTANI, 1981b) and *Gonatus* sp. of BUBLITZ, 1980. A form that probably represents an additional species occurs in Antarctic waters (YOUNG, 1972). *Gonatus phoebetriae* Imber, 1978, was described on the basis of a single lower beak. Because variation in the form of beaks within species is frequently broad (Fiscus, 1983, personal communication), and complete specimens are absent, I consider *G. phoebetriae* to be a *nomen dubium*, as does KRISTENSEN (1981).

MATERIALS AND METHODS

The material examined (Table 1) was collected by two separate research programs: one conducted by the University of Washington aboard the R/V *Brown Bear* (ARON, 1958, 1962) and the other conducted by the Oregon State University (O.S.U.) Nekton group aboard the R/V's *Yaquina* and *Cayuse* (e.g., PEARCY, 1964). Both sampling programs employed Isaacs-Kidd Midwater Trawls (ISAACS & KIDD, 1953) of various sizes (1.83, 2.44, 3.05 m depressor width) and configurations. Several of the O.S.U. Nekton samples were taken with Isaacs-Kidd Midwater Trawls (IKMT) that had multiple plankton samplers (MPS) as closing cod ends. The MPS was developed by BÉ (1962) and modified by PEARCY & HUBBARD (1964), PEARCY & MESECAR (1971), and PEARCY *et al.* (1977) to fish three or five nets at discrete subsurface depth horizons. Mesh size in the *Brown Bear* IKMT was 7.6 cm, with a 1.3 cm liner in the aft portion; the O.S.U. Nekton sampling program used 5 mm mesh in all but the cod end, which was 0.571 mm Nitex.

The samples were preserved in 10% buffered formalin-seawater solution at sea and transferred to fresh 5% buffered formalin in the laboratory before examination. Samples were subsequently transferred to 50% isopropyl alcohol, although often as long as 24 years after collection. The specimens were examined, enumerated, and measured to the nearest mm (or 0.5 mm, depending on dimension of the structure in question). Initial drawings were made with a *camera lucida*. The following counts and measurements were made, although not all measurements were always possible on all specimens. Measurements not further defined here correspond to those of VOSS (1956).

DML, dorsal mantle length
 MW, mantle width
 FL, fin length
 FW, fin width
 HW, head width
 ED, eye diameter, maximum diameter of bulbous
 AL I, length of arm I, measured from the base between arms I to the tip
 AL II, length of arm II, measured from the base between arms II and III to the tip
 AL III, length of arm III, measured from the base between arms III and IV to the tip
 AL IV, length of arm IV, measured from the base between arms IV to the tip
 TL, tentacle length, total length of tentacle stalk and club
 CL, club length, measured from basal sucker of carpus to tip of dactylus
 AH, arm hooks (present/absent)
 CH, largest (central) club hook (present/absent)
 OCH, other (than central) club hooks (number present/absent)
 DH, hook distal to large central club hook (present/absent)

PH, hooks proximal to large central club hook (number present/absent)

CS, total number of club suckers, counted from basal sucker of carpus to tip of dactylus

HAC I-IV, half arm count (number of suckers or suckers/hooks on the proximal half of arms I-IV)

Other abbreviations:

MWI, mantle width index = MW/DML

FLI, fin length index = FL/DML

FWI, fin width index = FW/DML

EDI, eye diameter index = ED/DML

TLI, tentacle length index = TL/DML

CLI, club length index = CL/DML

CAS, California Academy of Sciences, Department of Invertebrate Zoology, Golden Gate Park, San Francisco

OSUI, Oregon State University Invertebrate reference collection; College of Oceanography, Corvallis

USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Family GONATIDAE Hoyle, 1886

Characterized by a simple, straight funnel-locking cartilage; buccal connectives that attach ventrally to arms IV; tetraserial brachial armature, including two medial rows of hooks (except male *Berryteuthis anonychus*, which lack hooks).

Genus *Gonatus* Gray, 1849

Radula with five teeth in a transverse row; tentacles well developed, club with carpal-locking zone consisting of alternating ridges with large suckers medially and grooves with fleshy knobs medially.

Gonatus ursabrunae Jefferts, spec. nov.

(Figures 1, 2)

? *Gonatus fabricii* SASAKI, 1929 (*pars*):269-290, pl. 22, fig. 14; text fig. 128C.

Gonatus sp. A, JEFFERTS, 1983:88-93, including table 5 and fig. 31.

Material examined: **Holotype:** a juvenile of 24 mm DML; R/V *Brown Bear* cruise 235, haul 46; W. Aron and P. McCrery; south of Alaska Peninsula; 53°57'N, 157°39'W, 1.8 m IKMT fished open 0-225 m; 25 July 1959, 0129-0222 h; CAS 040163. **Paratype:** 1 juvenile, 20 mm DML; R/V *Brown Bear* cruise 235, haul 46; W. Aron and P. McCrery; south of Alaska Peninsula; 53°57'N, 157°39'W, 1.8 m IKMT fished open 0-225 m; 25 July 1959, 0129-0222 h; OSUI 701. **Paratype:** 1 juvenile, 19 mm DL; R/V *Yaquina* cruise YALOC 66, haul 849, south of Alaska Peninsula; 52°58.5'N, 162°48'W, 3.0 m IKMT-MPS fished open 0-2400 m; 6 July 1966, 0707-1330 h; USNM 816326. **Paratype:** 1 juvenile, 18 mm DML; R/V *Yaquina* cruise YALOC 66, haul 845; south of Alaska Peninsula; 54°58.2'N, 166°02'W, 1.8 m IKMT fished open

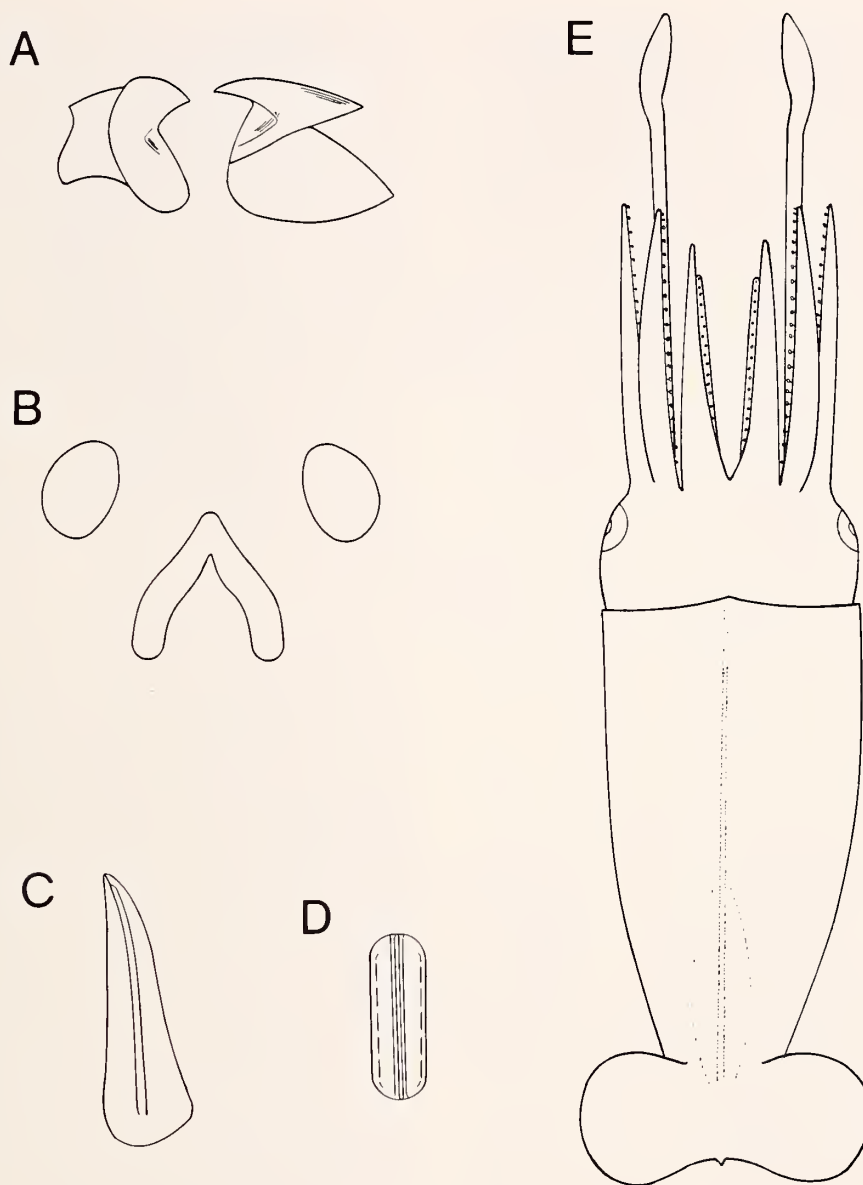


Figure 1

Gonatus ursabrunae spec. nov. A, lower and upper mandibles, CAS 057606, 17 mm DML. B-D, USNM 816236, 19 mm DML: B, funnel organ; C, funnel cartilage; D, nuchal cartilage. E, whole animal, dorsal aspect, OSUI 701, 20 mm DML.

0-200 m; 4 July 1966, 0240-0321 h; OSUI 696. **Paratype:** 1 juvenile, 17 mm DML; R/V *Yaquina* cruise YALOC 66, haul 849; south of Alaska Peninsula; 52°58.5'N, 162°48'W, 3.0 m IKMT-MPS fished open 0-2400 m; 6 July 1966, 0707-1330 h; CAS 057606. **Paratype:** 1 juvenile, 15 mm DML; R/V *Yaquina* cruise YALOC 66, haul 837; J. Donaldson; south of Adak Island; 50°32.3'N, 176°04.5'W, 1.8 m IKMT fished open 0-160 m; 22 June 1966, 0031-0107 h; CAS 057607. **Paratype:** 1 juvenile, 12 mm DML; R/V *Yaquina* cruise YALOC 66, haul 842; J. Donaldson; southeast of Adak

Island; 51°43.8'N, 175°20'W, 1.8 m IKMT fished open 0-200 m; 1 July 1966, 0309-0347 h; USNM 816325.

Additional material (all in the collections of Oregon State University): 2 juveniles, mantles missing; R/V *Yaquina* cruise YALOC 66, haul 843; J. Donaldson; south of central Aleutian Islands; 51°01.0'N, 171°32.0'W, 1.8 m IKMT fished open 0-200 m; 2 July 1966, 0305-0345 h; 1 juvenile, mantle missing; R/V *Yaquina* cruise YALOC 66, haul 850; J. Donaldson; south of Alaska Peninsula; 53°33.8'N, 160°08.0'W, 1.8 m IKMT fished open 0-160 m; 7 July 1966, 0125-0205 h; 3 juveniles, 23 mm DML,

2 missing mantles; R/V *Brown Bear* cruise 176, haul 34; Allen and P. McCrery; south of Alaska Peninsula; 52°29'N, 160°59'W, 1.8 m IKMT fished open 0–60 m; 1 August 1957, 0146–0222 h; 1 juvenile, 18 mm DML; R/V *Brown Bear* cruise 176, haul 85; P. McCrery, Semon, and Linger; south of Aleutian Islands; 51°26'N, 174°10'W, 1.8 m IKMT fished open 0–225 m; 24 August 1957, 0032–0124 h; 1 juvenile, 15 mm DML; R/V *Brown Bear* cruise 235, haul 23; W. Aron and P. McCrery; Gulf of Alaska; 52°49'N, 142°45.5'W, 1.8 m IKMT fished open 0–225 m; 20–21 July 1959, 2334–0028 h; 1 juvenile, 18 mm DML; R/V *Brown Bear* cruise 235, haul 44; W. Aron and P. McCrery; south of Alaska Peninsula; 53°55.5'N, 153°17'W, 1.8 m IKMT fished open 0–400 m; 24 July 1959; 0337–0454 h; 1 juvenile, 23 mm DML; R/V *Brown Bear* cruise 235, haul 45; W. Aron and P. McCrery; south of Alaska Peninsula; 53°56.5'N, 157°57.5'W, 1.8 m IKMT fished open 0–400 m; 25 July 1959, 0004–0119 h; 2 juveniles, 21, 25 mm DML; R/V *Brown Bear* cruise 235, haul 47; W. Aron and P. McCrery; south of Alaska Peninsula; 53°57'N, 157°49'W, 1.8 m IKMT fished open 0–60 m; 25 July 1959, 0223–0300 h; 1 juvenile, 22 mm DML; R/V *Yaquina* sta. NH-65; off Oregon coast; 44°43.3'N, 125°41.1'W, 1.8 m IKMT fished open 0–200 m; 14 February 1967, 0418–0500 h.

Description: Mantle plump, widest at anterior margin (MWI = 30–53, widest in small individuals; meristic indices summarized in Table 2), narrowing to pointed tip and adhering to gladius (Figure 1e). Mantle of soft consistency. Eyes large, occupying entire lateral surface of head (EDI = 18–21); anterior sinus small and broad. Ventral surface of mantle slightly emarginate at anterior edge. Fins relatively small, FWI = 41–58, FLI = 26–50, very thin, posteriorly attached just dorsal and anterior to the posterior tip of the gladius; posterior edge of fins united at midline, and projecting slightly posteriorly (Figure 1e). Funnel not extending as far as midpoint of eyes; in most specimens anterior tip of funnel not, or only just, visible at ventral margin of mantle (perhaps owing to contraction on preservation). Mantle-locking cartilage straight, slightly expanded posteriorly (Figure 1c). Dorsal component of funnel organ a broad inverted V, with expanded posterior lobes (Figure 1b). Ventral element of funnel organ a pair of small ovoid pads each about half the length of each branch of dorsal element. Funnel valve large and broad. Nuchal folds low and indistinct, no more than two folds observed on one side; the low and short olfactory papilla is just posterior to the eyes, in line with and anterior to the funnel-mantle locking cartilages.

Arm formula generally III \geq II > I \geq IV. Arms relatively short: ALI for longest arms (III or II) 42–56, ALI for shortest arms (IV) 25–44. Aboral keels well developed on arms IV. Trabeculate protective membranes very well developed on arms I–III, especially in larger individuals. Brachial armature quadriserial; suckers of the two medial rows small (0.18–0.20 mm diameter) in all individuals examined (largest individual examined, the holotype, was

24 mm DML). These medial suckers have about nine long, slender, blunt teeth on the inner distal margin (Figure 2c), those on the largest suckers reach about 0.024 mm in length, or approximately one-fifth of the diameter of the sucker opening. The two lateral rows of suckers are borne on trabeculae and consist of suckers that are greatly enlarged along the middle third of arms I–III (Figure 2f). The largest of these suckers are 0.50 mm in diameter and have 9–16 short, blunt teeth (much shorter than on suckers from the medial rows) on the distal inner margin (Figure 2d). Arms IV bear four rows of equally sized suckers (0.10–0.12 mm in diameter in holotype) which are smaller than the medial suckers of arms I–III. Half-arm counts for the two largest specimens are given in Table 3, but are not very consistent between the two specimens. It is extremely difficult to make accurate counts on smaller specimens. These counts of only two specimens are of little use by themselves; when a larger body of data becomes available such counts may show consistent differences between species.

Tentacles are of moderate length, TLI = 53–79, and the clubs are moderately short, CLI = 13–25 (Figure 2a). A dorsoaboral keel is present on the club from the level of the central hook (or enlarged sucker) to the tip of the dactylus. The medial zone of the manus contains a central hook in the holotype, and an enlarged central sucker in specimens of 19 and 20 mm DML, with three or four proximal suckers in all three specimens (Figure 2a). A carpal-locking zone consists of approximately five alternating ridges and suckers. The dorsal marginal zone contains suckers in four rows, and the ventral marginal zone bears four to five rows. The dactylus suckers are disposed in about six rows just distal to the central hook (or enlarged sucker), but these rapidly decrease to four regular rows which continue out the length of the dactylus to a circlet of small suckers at the tip. The suckers distal to the central hook number approximately 110 (full club sucker counts are impossible, as no mature specimens are available, and many of the proximal suckers remain as buds even in the larger specimens). The dactylus suckers just distal to the central hook reach a maximum diameter of 0.30 mm in the holotype, and decrease in size distally (Figure 2b). In other species of *Gonatus* (specimens of similar size were used where possible), dactylus suckers never approach this maximum size:

Species	DML	Sucker diameter
<i>californiensis</i>	112	0.25
<i>oregonensis</i>	46	0.20
<i>madokai</i>	40	0.14
<i>pyros</i>	35	0.14
<i>berryi</i>	30	0.13
<i>onyx</i>	26	0.08
<i>middendorffi</i>	35	buds
<i>madokai</i>	22	buds
sp. C of Kubodera	15	buds

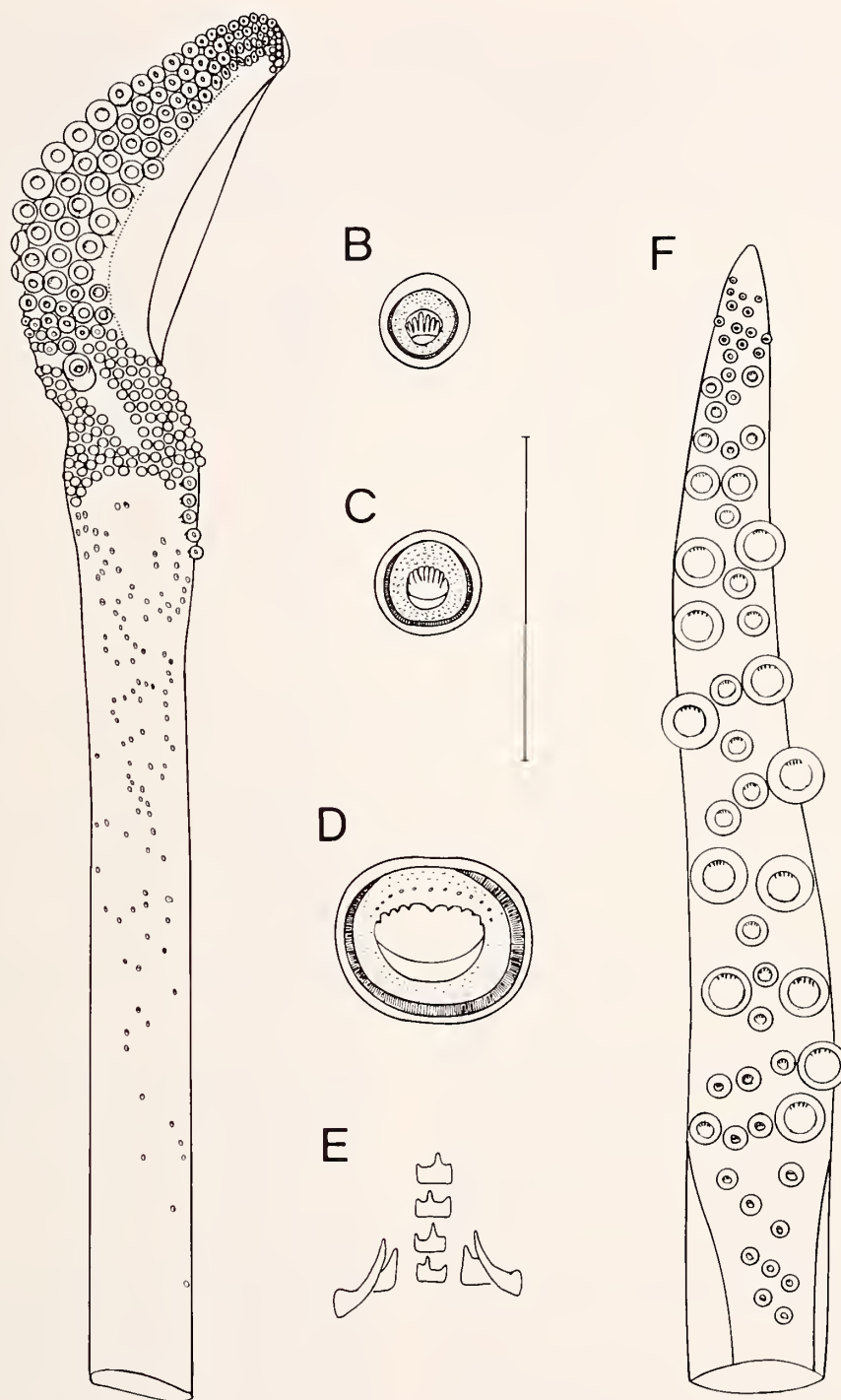


Figure 2

Gonatus ursabrunae. A-F, USNM 816326, 19 mm DML: A, tentacle; B, enlarged dactylus sucker; C, normal brachial sucker of medial row, A III; D, enlarged brachial sucker of lateral row, A III; E, radula; F, right arm III. Scale (B, C, D), 1 mm.

Table 1

Station data for the material examined, including type number (OSUI: 687-701. CAS: 040162-057608. USNM: 816325-816328. * indicates holotypes); station or haul number; date; latitude (N); longitude (W); gear depressor width of IKMT (m), or IKMT + MPS (hauls 2057#4, 2107#5, 2110#1 and #5); depth sampled (m); local time of sampling; and the vessel from which the sample was collected (Y, R/V *Yaquina*; B, R/V *Brown Bear*; C, R/V *Cayuse*).

Type no.	Haul no.	Latitude	Longitude	Gear	Date	Time	Depth	Vessel
<i>Gonatus ursabrunae</i>								
696	845	54°58.2'	166°02'	1.8	4 Jul 66	0240-0321	0-200	Y
700, 701	235-46	53°57'	157°39'	1.8	25 Jul 59	0129-0222	0-225	B
040163*	235-46	53°57'	157°39'	1.8	25 Jul 59	0129-0222	0-225	B
057606	849	52°58.5'	162°48'	3.0	6 Jul 66	0707-1330	0-2400	Y
057607	837	50°32.3'	176°04.5'	1.8	22 Jun 66	0031-0107	0-160	Y
816325	842	51°43.8'	175°20'	1.8	1 Jul 66	0309-0347	0-200	Y
816326	849	52°58.5'	162°48'	3.0	6 Jul 66	0707-1330	0-2400	Y
—	843	51°01.0'	171°32.0'	1.8	2 Jul 66	0305-0345	0-200	Y
—	850	53°33.8'	160°08.0'	1.8	7 Jul 66	0125-0205	0-160	Y
—	1016	44°44.4'	125°44.6'	1.8	14 Feb 67	0418-0500	0-200	Y
—	176-34	52°29'	160°59'	1.8	1 Aug 57	0146-0222	0-60	B
—	176-85	51°26'	174°10'	1.8	24 Aug 57	0032-0124	0-225	B
—	235-23	52°49'	142°46'	1.8	20 Jul 59	2334-0028	0-225	B
—	235-44	53°55.5'	153°17'	1.8	24 Jul 59	0337-0454	0-400	B
—	235-45	53°56.5'	157°57.5'	1.8	25 Jul 59	0004-0119	0-400	B
—	235-47	53°57'	157°49'	1.8	25 Jul 59	0223-0300	0-60	B
<i>Gonatus oregonensis</i>								
687	1011	44°46.2'	125°52.0'	1.8	13 Feb 67	1347-1728	0-1500	Y
690	2057#4	44°35.1'	125°32.5'	2.4	21 Jul 71	0314-0348	300-400	Y
692	2110#5	44°37.4'	125°41.3'	2.4	29 Nov 72	0327-0335	surface	Y
040162*	1692	44°39.1'	128°21.8'	1.8	21 Aug 69	0327-0414	0-240	C
057608	1563	44°40.2'	127°49.1'	1.8	30 Jun 69	2330-0020	0-220	Y
057609	2110#1	44°33.9'	125°39.2'	2.4	29 Nov 72	0105-0216	0-200	Y
816327	1091	44°40.9'	127°56.2'	1.8	3 Jun 67	2300-2343	0-185	Y
816328	2107#5	44°37.2'	125°42.3'	2.4	28 Nov 72	0641-0715	200-300	Y
—	884	44°54.2'	125°25'	1.8	25 Aug 66	0100-0540	0-2000+	Y
—	953	44°39.0'	125°41.4'	1.8	18 Dec 66	0042-0415	0-950	Y

Tentacle stalk suckers are small (about 0.04 mm diameter) and numerous. In a 19 mm individual, there are 25 suckers in the ventral row, 28 in the dorsal row, and 57 on the oral face between the two rows. In smaller individuals, the stalk suckers appear to be arranged in roughly six alternating rows. Measurements of the holotype and paratypes are given in Table 3.

Buccal connectives are attached dorsally to arms I and II and ventrally to arms III and IV. Seven short buccal lappets are present.

A spindle-shaped liver is present in smaller individuals, oriented obliquely to the body axis. Complete hook development is unknown, but the central hook develops at 20-24 mm DML; arm hooks and other club hooks may develop at sizes greater than 24 mm DML.

No trace of chromatophores remains on these specimens, most likely due to preservation. No photophores are present.

The radula (Figure 2e) is of the normal *Gonatus* type, with five rows of teeth: a tricuspid rhachidian, and simple admedian and lateral teeth on each side. No ridges are

visible on the teeth. The central tooth of the rhachidian is off-center, alternating sides with each row, *i.e.*, the teeth of the second and fourth rows are aligned, as are the teeth of the first and third rows.

The upper mandible is slightly curved and acutely pointed; both the upper and lower are pigmented only at the tips in a specimen of 19 mm DML (Figure 1a).

Type designation: The holotype is a juvenile of 24 mm DML. R/V *Brown Bear* cruise 235, station 46; W. Aron and P. McCrery; south of Alaska Peninsula, northeast Pacific; 53°57'N, 157°39'W; collected with a 1.8 m IKMT fished open 0-225 m; 25 July 1959, 0129-0222 h.

Location of type: California Academy of Sciences, Department of Invertebrate Zoology, Golden Gate Park, San Francisco. Catalogue number: CAS 040163.

Etymology: *ursabrunae*, after the vessel R/V *Brown Bear*, from which the holotype was collected.

Distribution: The known distribution is limited to the northeastern Pacific, but may extend into the northwest-

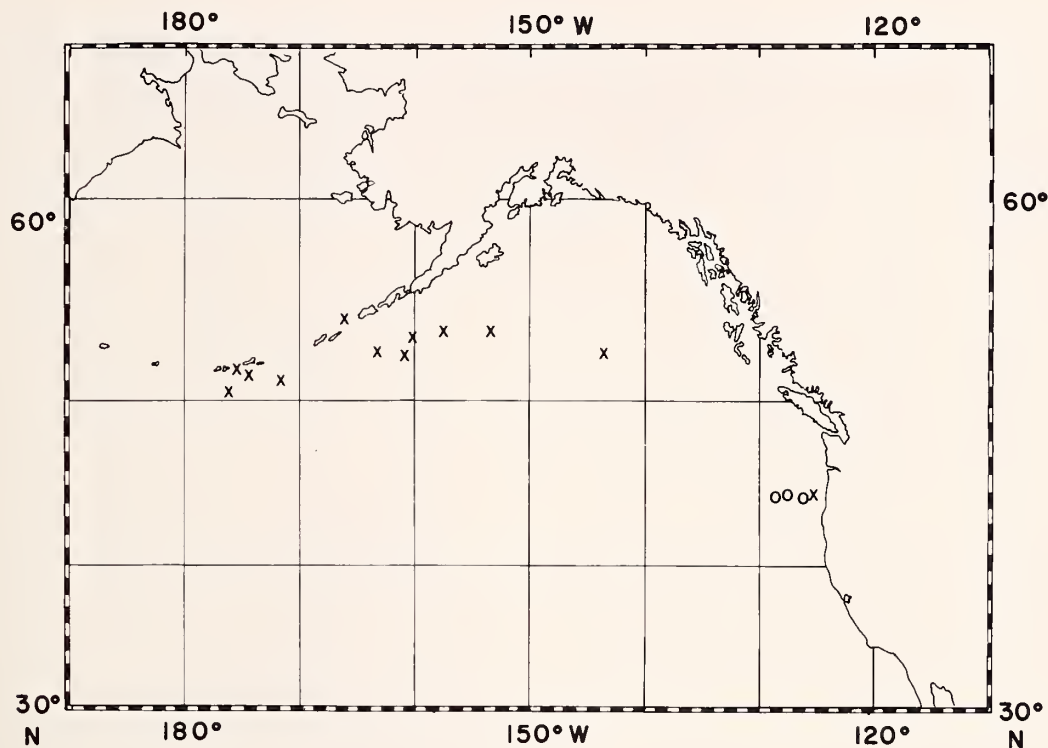


Figure 3

Location of hauls capturing *Gonatus ursabrunae* (x) and *Gonatus oregonensis* (o). For clarity, not all hauls are shown: three hauls captured *G. ursabrunae* in the area 53°56'–57'N, 157°39'–58'W; seven hauls captured *G. oregonensis* in the area 44°34'–54'N, 125°25'–52'W.

ern Pacific, considering Sasaki's specimen (see Discussion below). Twenty individuals have been collected in 14 mid-water hauls (all open; mostly 0–200 m; two hauls 0–400 m, one 0–2400 m; see Table 1) from the northern California Current and the Alaska Current as far west as 176°W (Figure 3). Okutani (*in litt.*, 1982) has seen three similar individuals in the collections of the University of Alaska. One was collected at Seward (60°N, 149°W), and the others in southeastern Alaska (56°N, 134°W; 58°N, 135°W).

Discussion: *Gonatus ursabrunae* clearly belongs in the genus *Gonatus* because of the structure of the radula and the development of a central hook on the tentacular club. Comparison of similarly sized specimens shows that it is not *G. pyros*, as it lacks an optic photophore, nor is it *G. berryi*, as no arm hooks are yet evident, as they are in juvenile *berryi*; neither can it be *G. tinro*, as it does have a club hook. Comparably sized individuals are known for *G. onyx*, *G. madokai*, *G. californiensis*, *G. middendorffi*, and *Gonatus oregonensis* (spec. nov., described and discussed below); none of these demonstrates the enlarged brachial and club suckers characteristic of this species. BUBLITZ (1980:76) stated that some of his specimens of *Gonatus* type A (which was described as *G. middendorffi*, KUBODERA

& OKUTANI, 1981a) showed slightly enlarged suckers in the lateral arm rows ("1.5–2 times as large as the corresponding median sucker"); however, his figure (pl. 30) clearly shows just the reverse, that the median sucker (transforming into a hook) is larger than the lateral sucker. These specimens otherwise agree with the description of *G. middendorffi*, which is separable from *Gonatus ursabrunae* by its MWI and the size at which club hooks develop. There are other differences, especially in club armature, which serve equally well to differentiate all of these species (Tables 4, 5). *Gonatus* type C of KUBODERA, 1978, is known from individuals as large as 16 mm DML; there is no indication of enlarged suckers in these, and this type is further characterized by a separated epidermis, which does not occur in *Gonatus ursabrunae*. BUBLITZ's (1980) new species also has no indication of enlarged suckers in the lateral rows: "each sucker of the median two rows is about 1.2 times as large as the corresponding lateral sucker" (BUBLITZ, 1980:61), and has five rows of sucker buds on the tentacular stalk as opposed to six in larvae of *G. ursabrunae*. The tentacles of Bublitz's species are shorter (TLI = 37–49) but have clubs of about the same size (CLI = 18–24); in addition, the ventral marginal zone comprises 3 or 4 rows of suckers in Bublitz's species, *vs.* 4 or 5 in *G. ursabrunae*. Several other differ-

Table 2

Meristic indices for *Gonatus ursabrunae*. Abbreviations as in methods section, with additions: ALIM, arm length index for longest arm (length of arm over DML \times 100); \bar{X} , mean; SD, standard deviation.

Index	Type no.							Range	\bar{X}	SD
	040163	701	816326	696	057606	057607	816325			
DML	24	20	19	18	17	15	12	12-24	17.9	3.80
MWI	33	30	42	44	53	40	42	30-53	40.6	7.52
FLI	21	20	21	22	18	20	17	17-22	19.9	1.77
FWI	46	45	53	56	41	53	58	41-58	50.3	6.32
HWI	29	36	26	33	29	33	33	26-35	31.1	3.18
EDI	21	20	21	19	18	20	21	18-21	20.0	1.15
ALIM	42	45	47	56	53	47	50	42-56	48.6	4.79
TLI	79	60	63	—	71	53	67	53-79	65.5	9.03
CLI	21	25	21	—	18	13	—	13-25	19.6	4.45

ences in tentacle sucker counts and disposition are evident: suckers distal to the central hook number approximately 85 in Bublitz's species (22 mm DML), but about 110 in *G. ursabrunae* (19 mm DML); suckers of the dorsal row, ventral row, and oral face of the tentacular stalk number about 15, 10, and 0 in Bublitz's species (22 mm DML), but 28, 25, and 57, respectively, in *G. ursabrunae* (19 mm DML).

SASAKI (1929) included one larva (pl. 22, fig. 14; text fig. 128C) in the description of *Gonatus fabricii* which appears to correspond to *Gonatus ursabrunae*. Measurements of this individual have been included here, in Table 3. SASAKI (1929:269) noted: "The suckers of the first three

pairs of arms, uniform, except in the largest larva referred to, where the suckers of the outer two series on these arms are much larger than those of the inner two series." In addition, he noted that the proximal suckers on arms IV were also enlarged, and numbered from two to seven, in the larvae of *G. fabricii*, although it is not clear from the description to which specimen(s) he was referring. No such condition has been noted for *Gonatus ursabrunae*. The geographical origin of Sasaki's specimen is unknown; it apparently came from collections of the *Albatross*, and SASAKI (1929:270) listed the following localities from which the *Albatross* collected *G. fabricii*: "Milne Bay, Simushir I., Kurile group; Bowers Bank, Bering Sea; near Near

Table 3

Measurements (in mm) of selected individuals of *Gonatus ursabrunae*. "Sasaki" refers to the specimen described by SASAKI (1929) which is discussed in the text. Type no.: 040163, 057606, 057607 are CAS; 696, 701 are OSUI; 816325, 816326 are USNM. ES, enlarged sucker.

Index	Type no.							Sasaki
	040163	701	816326	696	057606	057607	816325	
DML	24	20	19	18	17	15	12	14
MW	8	6	8	8	9	6	5	6.5
FL	5	4	4	4	3	3	2	—
FW	11	9	10	10	7	8	7	—
HW	7	7	5	6	5	5	4	—
ED	5	4	4	3.5	3	3	2.5	—
AL I	7	6	7	8	6	6	5	3.5
AL II	9	9	8	10	8	7	6	4
AL III	10	9	9	10	9	7	6	4
AL IV	8	6	6	8	6	5	3	2.5
TL	19	12	12	—	12	8	8	7
CL	5	5	4	—	3	2	?	?
AH	—	—	—	—	—	—	—	—
CH	—	ES	ES	—	—	—	—	—
OCH	—	—	—	—	—	—	—	—
HAC I	18	23	—	—	—	—	—	—
HAC II	25	19	—	—	—	—	—	—
HAC III	22	20	—	—	—	—	—	—
HAC IV	30	27	—	—	—	—	—	—

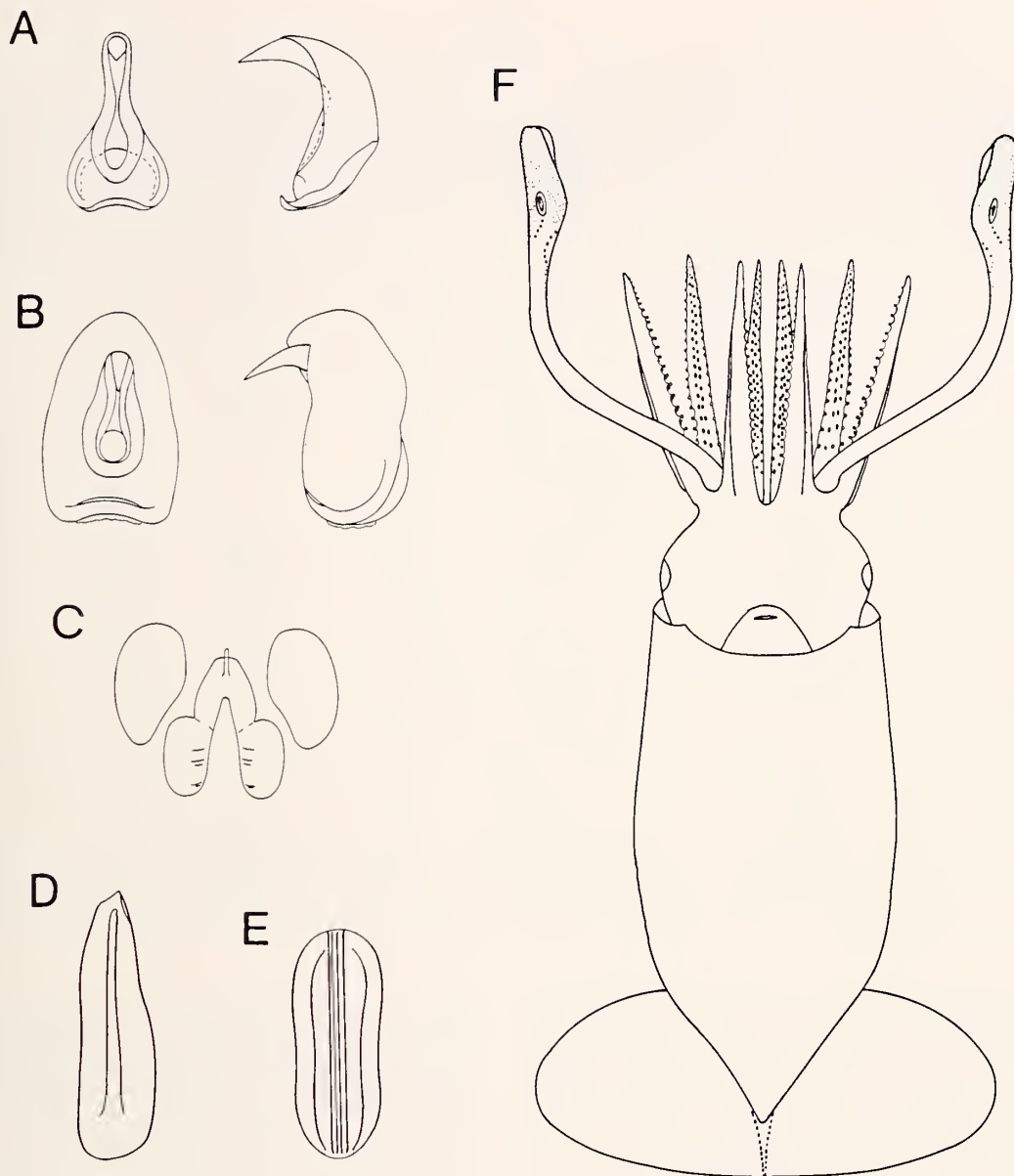


Figure 4

Gonatus oregonensis spec. nov. A-E, USNM 816327, 46 mm DML: A and B, hook of right arm III, with hood removed and with hood intact, front and lateral views; C, funnel organ; D, funnel cartilage; E, nuchal cartilage. F, whole animal, ventral aspect, CAS 057608, 31 mm DML.

Is., Aleutians; east of Kamchatka; south of Alaska; and near Commander Is."

Gonatus oregonensis Jefferts, spec. nov.

(Figures 4, 5)

Gonatus sp., E. JEFFERTS, 1983:94-98, including table 6 and fig. 31.

Material examined: **Holotype:** a juvenile of 39 mm DML; R/V *Cayuse* haul 1692; R. Findley; off the coast

of Oregon; 44°39.1'N, 128°21.8'W, collected with a 1.8 m IKMT fished open 0-240 m; 21 August 1969, 0327-0414 h; CAS 040162. **Paratype:** 1 juvenile, 46 mm DML; R/V *Yaquina* haul 1091; R. Eagle; off Oregon coast; 44°40.9'N, 127°56.2'W, 1.8 m IKMT fished open 0-185 m; 3 June 1967, 2300-2343 h; USNM 816327. **Paratype:** 1 juvenile, 35 mm DML; R/V *Yaquina* haul 1011; off Oregon coast; 44°46.2'N, 125°52.0'W, 1.8 m IKMT fished open 0-1500 m; 13 February 1967, 1347-1728 h; OSUI 687. **Paratype:** 1 juvenile, 31 mm DML; R/V

Table 4

Comparison of species of the family Gonatidae from the North Pacific. Adult characters (indices for animals over 40 mm DML), including known size range (DML in mm), number of teeth in transverse row of radula, shape of nuchal cartilage, photophores, mantle width index, maximum arm length index, size at which arm hooks develop (DML in mm), hook and sucker pattern on club (*e.g.*, hHhhh is one distal hook, a large central hook, and three proximal hooks), size (DML in mm) at which the central, distal, and proximal hooks develop, rows of suckers on the dactylus (from just distal to the hooks toward the end—in *Berryteuthis*, the manus is included; Irr, irregular), number of suckers on the club,

Species	Known size range	Teeth on radula	Nuchal cartilage	Photophores	MWI	ALIM	Arm hooks
<i>Gonatus</i>							
<i>ursabrunae</i>	12–30	5	rectangular	none	—	—	>24
<i>pyros</i>	7–66	5	rectangular	optic	26	64	17–22
<i>berryi</i>	6–119	5	rectangular	none	25–35	64–72	7–9
<i>tinro</i>	7–89	5	rectangular	none	20	64	19–21
<i>onyx</i>	2–98	5	rectangular	none	21–27	50–59	26–28 or 18–20
<i>madokai</i>	6–329	5	rectangular	none	23–30	90–103	16–19
<i>middendorffi</i>	6–296	5	rectangular	none	18–22	40–52	20–30 or 26–30
<i>oregonensis</i>	24–46	5	rectangular	none	26	63	24–30
<i>californiensis</i>	24–112	5	rectangular	none	19–33	46–55	26–29
sp. C of Kubodera	4–16	5	? rectangular	none	—	—	>16
sp. of Bublitz	7–80	5	rectangular	none	33–35	63–65	21–38
<i>Gonatopsis</i>							
<i>borealis</i>	4–290	7	panduriform	none	22–39	44–67	30–35
<i>Berryteuthis</i>							
<i>anonychus</i>	5–99	7	panduriform	none	21–29	30–33	? >30
<i>magister</i>	6–320	7	panduriform	none	27–29	62–68	>16 or 55–60

Yaquina haul 1563; P. Kalk and D. Stein; off Oregon coast; 44°40.2'N, 127°49.1'W, 1.8 m IKMT fished open 0–220 m; 30 June–1 July 1969, 2330–0220 h; CAS 057608. **Paratype:** 1 juvenile, 30 mm DML; R/V *Yaquina* haul 2057#4; W. Pearcy; off Oregon coast; 44°42.4'N, 125°32.5'W, 1.8 m IKMT fished open 0–600 m; 21 July 1971, 0314–0348 h; OSUI 690. **Paratype:** 1 juvenile, 30 mm DML; R/V *Yaquina* haul 2107#5; off Oregon coast; 44°37.2'N, 125°42.3'W, 3.0 m IKMT + MPS fished 300–200 m; 28 November 1972, 0641–0715 h; USNM 816328. **Paratype:** 1 juvenile, 30 m; R/V *Yaquina* haul 2110#1; off Oregon coast; 44°33.9'N, 125°39.2'W, 3.0 m IKMT + MPS fished 0–200–150 m; 29 November 1972, 0105–0216 h; CAS 057609. **Paratype:** 1 juvenile, 24 mm; R/V *Yaquina* haul 2110#5; off Oregon coast; 44°37.4'N, 125°41.3'W, 3.0 m IKMT + MPS fished at surface; 29 November 1972, 0327–0335 h; OSUI 692.

Additional material (all in the collections of Oregon State University): 1 juvenile, 26 mm DML; R/V *Yaquina* haul 953; station NH-50; Coleman; off Oregon coast; 44°38.8'N, 125°20.7'W, 1.8 m IKMT fished open 0–950

m; 18 December 1966, 0042–0415 h; 1 juvenile, 19 mm DML; R/V *Yaquina* haul 884; station WG-16; Coleman and Wyandt; off Oregon coast; 44°54.2'N, 125°25'W, 1.8 m IKMT fished open 0–2000 m; 25 August 1966, 0100–0540 h.

Description: Mantle plump, widest in the midsection (MWI = 29–43; meristic indices are summarized in Table 6). Ventral anterior margin of mantle emarginate (Figure 4f). The corners of this emargination project at the anterior ends of the mantle-locking cartilages. Head less wide than mantle, with at least two nuchal folds. Eyes are large, occupying the entire lateral surfaces of head (EDI = 15–23); an optic sinus is at the anterior end, between the bases of the tentacle and arm III.

Fins broad but relatively short: FWI = 80–90 for animals over 30 mm DML; FLI = 25–45. Fins united posteriorly, extending beyond the tip of the gladius. A cartilaginous end cone extends to the posterior limit of the fins. Posterior margin of fins essentially straight, anterior margin convex. Margins quite thin, fragile, especially anteriorly.

Table 4
Continued.

and the sucker distribution pattern on the tentacular stalk (*e.g.*, 1V, 1-2, 1D represents one row of suckers along ventral margin, 1-2 suckers on medial face, and 1 row along dorsal margin of the stalk). Abbreviations as in Table 3. From original data and NESIS (1972), YOUNG (1972), KUBODERA & OKUTANI (1977, 1981a, b), BUBLITZ (1980), BUBLITZ & NISHIYAMA (MS).

Club formula	C Hook	D Hook	P Hooks	Rows on dactylus	Club suckers	Stalk pattern
?H??	20-24	? (>24)	? (>24)	6->4	194+	1V, 57, 1D
hHhhhh	15-18	18-23	21-26	Irr->4	159-181	2V, 50-125, 1D
hHsshhhh	12-17	19-28	25-32	4	162-178	1V, 1-2, 1D
no hooks	—	—	—	5-6->18 >12->4-5	576-600	—
sHsssss or hHsssss	17-24	—	—	5-6->4	165-194	1V, <10, 1D
hHhhhhh	>72	>72	>72	5-6->4	215+	2V, few, 1D
hHsssss or hHshhss	>60	>60	>250	7-8->4	340	1V, few, 1D
hHhhhhss	24-30	24-30	35-39	7-8->5-6	295-370	1V, 63-74, 1D
hHhhhs	17-23	24-30	35-41	7-8->4	217-269	1V, 40-80, 1D
-S--	—	? (>16)	? (>16)	—	buds	—
hHhhhhh	13-15	>22	22-38	5-6->4	183	1V, none, 1D
—	—	—	—	—	55 max	—
no hooks	—	—	—	13->4	650-738	—
no hooks	—	—	—	16->4	1106-1273	—

Funnel reaching only slightly past the posterior extent of the eye. Funnel-locking cartilage slightly curved laterally, with a shallow medial groove which widens caudad, and with a distinct anterior fold, corresponding to a projection on the ventral surface of the mantle (Figure 4d). Funnel valve small and broad. Dorsal pad of funnel organ very broad, with an anterior papilla and narrow ovoid pads at the posterior ends of the arms (Figure 4c). General shape that of an inverted V, but with posterior portions of arms laterally offset from anterior portions. Ventral component of funnel organ consists of two broadly ovoid pads each nearly as long as the arms of the dorsal pad. Nuchal cartilage only slightly clavate, and slightly wider at anterior end. The cartilage has a narrow medial ridge with a medial groove, and broad lateral grooves (Figure 4e).

Arms of moderate length, ALI = 59-63 in 46 mm DML individual, 43-53 in 30 mm DML individual. Arm formula generally III \geq II > IV \geq I. Aboral keels are strong and nearly always evident on arms IV; they are occasionally discernible on arms I-III. Trabeculate protective membranes are exceedingly well developed on arms I-III;

the marginal rows of suckers are borne on the trabeculae. Arms I-III bear hooks in the medial rows (Figures 4a, b, 5); these develop at a mantle length of 24-30 mm. Arms IV bear four rows of suckers. Lateral suckers of arms I to III relatively small, with about eight closely set, elongate, blunt teeth (Figure 5d). Half-arm counts for two of the larger individuals are given in Table 7.

The tentacle is long, TLI = 60-105 (depending on preservational state), and bears a fairly large club (CLI = 21-20). A swimming keel is present on the dorsal surface of the dactylus, extending from the level of the distal hook to the tip of the dactylus (Figure 5g). Dorsal and ventral protective membranes are also present, but are very short and ill-developed. They originate on the stalk and extend along the club to its tip. The club bears a large central hook, a distal hook about half the size of the central one, and several proximal hooks. The central and distal hooks develop at a DML of about 24-30 mm, but the proximal hooks are not evident until a length of 35-39 mm is attained. In the proximal series (Figure 5f), the suckers next to the central hook are the first to transform into hooks, so that an animal of 39 mm may have two hooks proximal

Table 5

Comparison of early life history stages of species of the family Gonatidae. Characters for individuals under 40 mm DML, including size range of specimens included (mm DML), mantle width index, maximum arm length index, rows of suckers on tentacular stalk in larval forms (these suckers are lost as the club begins to develop), tentacle length index, and club length index. Information from original data and NESIS (1972), YOUNG (1972), KUBODERA & OKUTANI (1977, 1981a, b), BUBLITZ (1980), and BUBLITZ & NISHIYAMA (MS). (BUBLITZ, 1981, measured stretched mantle width).

Species	Size range	MWI	ALIM	Rows of stalk suckers	TLI	CLI
<i>Gonatus</i>						
<i>ursabrunae</i>	12-24	24-53	42-56	6	50-79	13-25
<i>pyros</i>	13-25	42	38-48	5-6	52	21
<i>berryi</i>	13-30	30-33	48	5-6	35-100	25
<i>tinro</i>	10-28	35-47	34-74	5-6	40	10-15
<i>onyx</i>	6-26	35-40	35-40	5	25-55	20-25
<i>madokai</i>	10-40	30-35	30-80	4-5	30-90	12-15
<i>middendorffi</i>	6-40	24-40	25-45	4	30	15
<i>oregonensis</i>	24-39	29-43	42-67	6	60-105	21-30
<i>californiensis</i>	29-38	29-32	41-47	?	66-82	21-24
sp. C of Kubodera	6-16	40-50	30	5-6	50-75	4-8
sp. of Bublitz	11-13	35-61	23-55	5	41-75	18-34
	16-22	42-45	37-59	5	37-49	18-24
<i>Gonatopsis</i>						
<i>borealis</i>	5-30	30-40	25-40	4-5	25-30	—
<i>Berryteuthis</i>						
<i>anonychus</i>	5-30	25-45	33-40	3-4	~50	7-18
<i>magister</i>	7-16	40-45	35-40	5-6	50	5-13

to the central, and three to four suckers, and an animal of 46 mm may have four hooks proximal to the central, and two suckers.

The carpal-locking zone consists of four to five ridges with accompanying suckers, alternating with five to six knobs. This series extends onto the stalk. The ventral marginal zone contains four rows of suckers and the dorsal marginal zone five. The tentacular stalk bears single rows of suckers on both the ventral and dorsal margin of its inner face. The space between the rows is beset with many

small suckers. The number of suckers in the ventral row is at least 74 in the 46 mm specimen, in the dorsal row, at least 63, and on the medial face, at least 70. In a 24 mm specimen, the stalk suckers appear to be arranged in six, somewhat irregular, alternating rows.

The dactylus bears many small but roughly equal-sized suckers (0.20 to 0.25 mm at DML 46 mm). These have narrow openings and four to six long, slender, peglike teeth on the distal border of the inner ring (Figure 5e) and are disposed in seven or eight rows just distal to the

Table 6

Meristic indices for *Gonatus oregonensis*. Abbreviations as in Table 2.

Index	Type no.								Range	\bar{X}	SD
	816327	040162	687	057608	690	816328	057609	692			
DML	46	39	35	31	30	30	30	24	24-46	33.1	6.77
MWI	35	31	29	42	33	43	33	38	29-43	35.5	5.07
FLI	48	44	34	32	40	40	40	33	32-48	38.9	5.59
FWI	89	82	80	81	83	83	83	58	58-89	79.9	9.23
HWI	22	28	31	29	30	23	30	25	22-31	27.2	3.45
EDI	16	22	—	19	23	15	20	17	15-23	18.9	3.02
ALIM	63	64	54	58	53	60	67	42	42-67	57.6	7.95
TLI	96	69	80	81	63	107	103	75	63-107	84.2	16.1
CLI	26	23	26	23	27	30	30	21	21-30	25.8	3.28

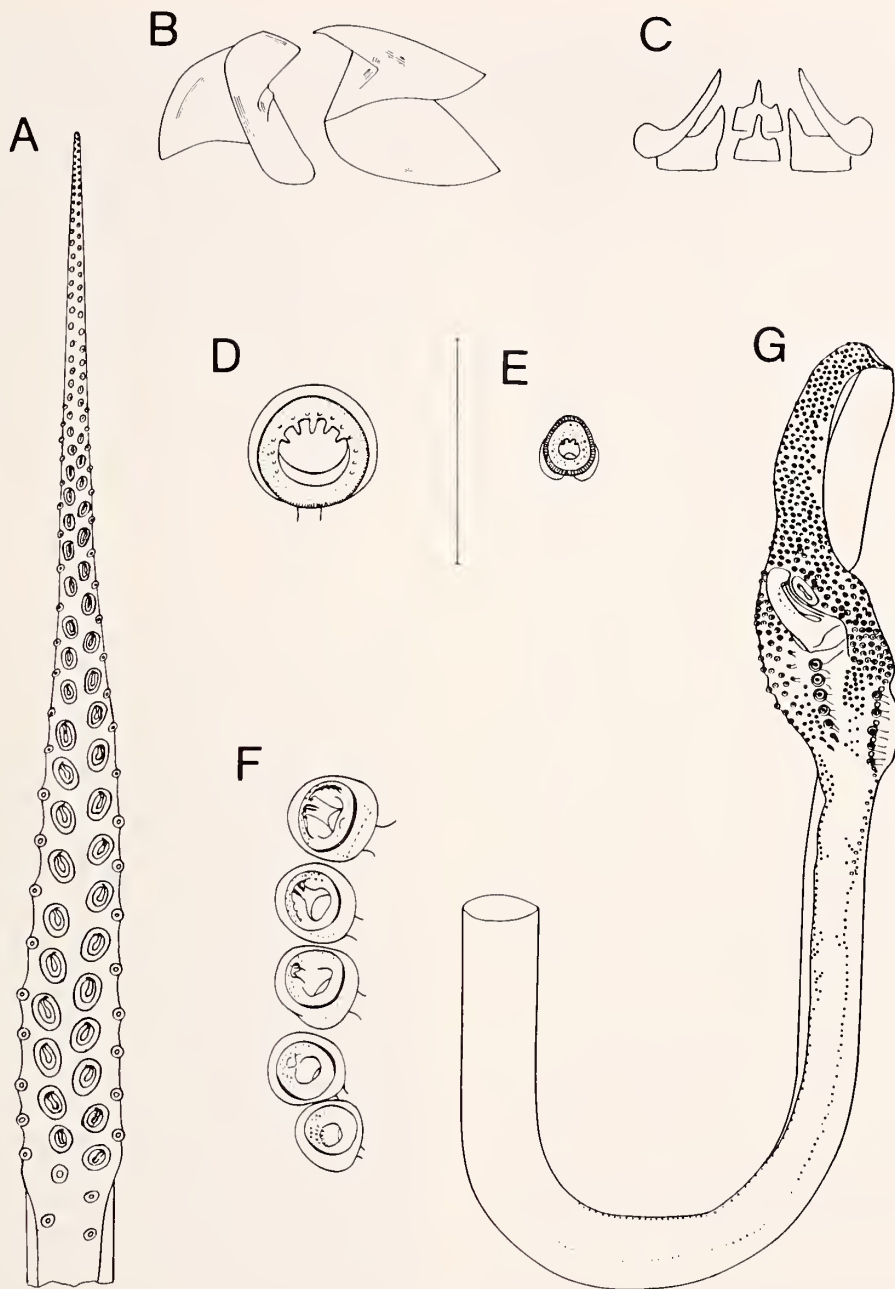


Figure 5

Gonatus oregonensis. A, right arm III, USNM 816327, 46 mm DML. B, C, OSUI 687, 35 mm DML: B, mandibles; C, radula. D–G, USNM 816327, 46 mm DML: D, brachial sucker, right arm III; E, dactylus sucker; F, proximal series of club; G, tentacle. Scale (D and E), 1 mm.

hooks, decreasing to five or six rows near the tip (Figure 5g). A cirlet of small suckers occupies the tip of the dactylus. The total number of suckers on the dactylus, ventral marginal zone, and dorsal marginal zone is 320 in the 46 mm specimen, and shows a range of 295 to 370 in the other specimens.

Buccal connectives are connected to dorsal borders of arms I and II and to the ventral borders of arms III and IV.

The radula is of the normal quinquedentate *Gonatus* type, with tricuspid rhachidian, unicuspid admedian, and unicuspid lateral. No ridges are apparent on the radular

Table 7

Measurements (in mm) and counts for selected individuals of *Gonatus oregonensis*. Type no.: 040162, 057608, 057609, CAS; 687, 690, 692, OSUI; 816327, 816328, USNM. D, damaged; +, present; -, absent or not applicable.

Haul: type no.:	1091 816327	1692 040162	1011 687	1563 057608	2057#4 690	2107#5 816328	2110#1 057609	2110#5 692
Index								
DML	46	39	35	31	30	30	30	24
MW	16	12	10	13	10	13	10	9
FL	22	17	12	10	12	12	12	8
FW	41	32	28	25	25	25	25	14
HW	10	11	11	9	9	7	9	6
ED	7.5	8.5	D	6	7	4.5	6	4
AL I	27	22	16	15	13	13	15	8
AL II	28	25	19	18	15	16	19	10
AL III	29	24	19	17	16	18	20	10
AL IV	28	18	17	14	13	14	18	9
TL	44	27	28	25	19	32	31	18
CL	12	9	9	7	8	9	9	5
AH	+	+	+	+	+	+	+	-
CH	+	+	+	+	+	+	+	-
DH	+	+	+	+	+	+	+	-
PH	4	2	-	-	-	-	-	-
CS	320	347	339	355	370	295	320	300
HAC I	20/14	-	17/5	-	-	-	-	-
HAC II	22/15	-	19/9	-	-	-	-	-
HAC III	19/15	-	17/9	-	-	-	-	-
HAC IV	47	-	35	-	-	-	-	-

teeth, and the central teeth of the rhachidian are aligned in each row (Figure 5c).

The upper mandible is long and acute; both upper and lower mandibles are darkly colored only on the tips in a specimen of 46 mm (Figure 5b).

Type designation: The holotype is a juvenile of 39 mm DML. R/V *Cayuse*, haul 1692; Findley; off the coast of Oregon; 44°39.1'N, 128°21.8'W; collected with a 1.8 m IKMT fished open 0-240 m; 21 August 1969, 0327-0414 h.

Location of type: California Academy of Sciences, Department of Invertebrate Zoology, Golden Gate Park, San Francisco. Catalogue number: CAS 040162.

Etymology: *oregonensis*, after the type locality; to emphasize the morphological similarity to another species localized in the California Current, *G. californiensis*.

Distribution: This species is currently known only from waters off Oregon. Ten individuals were collected in ten midwater hauls (all open, mostly 0-400 m; one 0-1500 m, one 0-2000 + m) in the northern portion of the California Current system (Figure 3). Measurements for eight of these are given in Table 7.

Discussion: This species is easily separable from all but one of the described species of *Gonatus* (Table 4, 5). The distribution of hooks on the club separates it from *G.*

berryi (in which the proximal hooks are separated from the central hook by one or two suckers), from *G. onyx* (no proximal hooks), and from *G. tinro* (no club hooks). *Gonatus pyros* has an optic photophore, and *G. madokai* has only eight to ten minute suckers on the oral face of the tentacular stalk (several other characters also serve to separate these species). *Gonatus middendorffi* develops all club hooks at a much larger size (over 60 mm DML), and has a more slender body. *Gonatus* sp. of BUBLITZ (1980) has fins which are somewhat less broad (FWI = 43-87 vs. 80-89 in *Gonatus oregonensis*), and shows significant differences in the number and disposition of club suckers (probably fewer than 100 club suckers in *Gonatus* sp. of BUBLITZ, 1980, arranged in four rows on the dactylus).

This species is less easily separable from *Gonatus californiensis*. The distribution of hooks on the club is the same in the two species, and the size at which all hooks develop is similar. There are, however, consistent differences in fin dimensions, in sucker counts on the club, and in distribution of suckers on the dactylus. My present collection does not contain mature individuals; these differences may be better characterized on examination of larger individuals. YOUNG's (1972) specimens of *Gonatus californiensis* (29-112 mm DML) showed a FWI = 54-70. Specimens of *G. oregonensis* 30 mm and over had a FWI = 80-89. The clubs are also somewhat larger in *G. oregonensis*: CLI = 21-30 vs. 17-24 in *G. californiensis*. Club sucker counts show no overlap in the two species:

G. oregonensis ranges from 295 to 370, and Young's *G. californiensis* from 217 to 269. In *Gonatus oregonensis*, suckers are arranged in seven to eight rows at the base of the dactylus, and decrease to five to six rows at the tip. In *G. californiensis*, the dactylus suckers are disposed in eight rows basally and "decrease to four rows about halfway out on the dactylus" (YOUNG, 1972:52). The arms are also noticeably longer in *G. oregonensis* than in *G. californiensis*: at 46 mm DML, the longest arms (III and II) are 23–24 mm in *G. californiensis* and 28–29 mm in *G. oregonensis*. Further comparison supports this difference (the data for *G. californiensis* are from YOUNG, 1972):

Arm length index for longest arms (II, III)

DML	<i>californiensis</i>	<i>oregonensis</i>
46 mm	50–52	61–63
38–39	47	62–64
34–35	47	54
29–30	41	50–67

This new form thus represents an intermediate condition between *Gonatus tinro*, which has a *Berryteuthis*-like club with no hooks but many (>400) suckers, and *G. californiensis*, *G. pyros*, and *G. madokai*, which have central, distal, and proximal hooks, but fewer (<270) suckers on the club. I believe that this form represents a distinct species, as several characters show no overlap with *G. californiensis*: fin dimensions, arm length, and sucker number and distribution on the club.

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